CHAPTER 2

THE QUESTION OF COMMERCIALIZING TRANSGENIC CONIFERS

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Abstract. Genomics is creating new knowledge in forestry and making novel transgenic forest trees is one of its many emerging economic deliverables. What is the decision matrix for using transgenic conifers on a commercial scale? Three major determinants will shape decisions to use plant transgenic forest trees on a commercial scale: reproductive biology of the forest species, production systems and the type of transgene. One example is given as a case study of *Pinus taeda* in the southeastern United States. Exploring likely scenarios for commercial use suggested the need for a public-private technology partnership or technology trust. A technology trust proposed for transgenic *Pinus taeda* has three components for gathering sound information about transgenic conifer use: 1) a gene conservation program as a hedge against molecular domestication which would be subsidized by 2) a technology tax on transgenic field testing which includes a hold-harmless provision for the payee and 3) a public-private partnership for evaluating benefits-risks analysis which would also serve as an outlet for public deliberation.

1. INTRODUCTION

High throughput genomics is providing a wealth of new DNA sequences available for gene discovery and genetic modification in plants. Forest trees are no exception. Genomics and gene discovery, when combined with clonal technology, offers the opportunity for capital accumulation through production of transgenic trees as one of many applications. And pursuit of transgenic technology research is principally corporate, shaped by the imperatives of private investment, market forces and government regulatory institutions. In simplest terms, novel forest tree phenotypes can now be created on a commercial scale as a means to increase shareholder value of investor companies so biotechnology firms are preparing for commercial use in the near future. From the vantage point of societal good, transgenic forest trees are appealing as a new way to meet the world's need for higher-yielding forests while reducing the pressure on more fragile ecosystems.

Concerns about these justifications for transgenic forest trees surface in the absence of relevant ecological risk information. First, use of transgenic trees on a commercial scale means potential benefits will accrue to shareholders yet its ecological risks, if any, will be shouldered by all citizens. Second, using transgenic trees as part of the high-yield forest management technology portfolio without gauging its ecological impact opens the prospect of doing harm to the very ecosystems it purports to protect. Better information about ecological risks on a case-by-case basis is needed although public awareness tends to low.

Ecological risk analysis has not paralleled recent breakthroughs in transgenic technology for conifers. Long-distance dispersal for conifer pollen has been observed empirically for over a hundred years (BESSEY 1884) compared to the recent advent of genetic transformation for a conifer less than 20 years ago (SEDEROFF *et al.*, 1988). A couple of reasons are offered: 1) the distinctions between transgenic conifers and transgenic food crops are so poorly understood to the extent that gene flow questions for conifers do not command research priority in agricultural funding programs and 2) the concentration of private investment in transgenic conifer research and development means that no formal outlet exists for public deliberation or policy debates which in turn would raise public awareness. This is consistent with the observation that national forests, not private forests, have been the playing field for debates about genetic composition (FRIEDMAN AND FOSTER 1997).

1.1. Distinctions between transgenic conifers and transgenic food crops

If transgenic conifers are traditionally viewed as another type of transgenic agricultural crops then we must consider the possibility that the question of ecological risk has become passé even before transgenic conifers were feasible on a commercial scale. Extensive gene flow studies from transgenic crops have been conducted; one outcome has been deregulation for many crop species. Another outcome is that those transgenic crops still under regulation are surrounded by biocontainment zones to prevent transgenic pollen escape. But gene flow is more complex for conifers than annual plants and biocontainment zones are ineffective (WILLIAMS 2005; WILLIAMS et al., 2006). Few public policy decision makers have delved into these distinctions. Unless the question of ecological risks for transgenic conifers is treated separately from those associated with food crops, it is reasonable to expect that tensions will escalate between private and public interests. If so, the question of commercialization, pro or con, will remain mired for lack of relevant information.

1.2. Determinants for ecological risks associated with transgenic conifers

Gene flow for forest trees is complex, occurring on micro-, meso and macro-transport scales. Seeds and pollen can move kilometers from source with 100% certainty (WILLIAMS *et al.*, 2006). In the most recalcitrant cases, each transgenic conifer can produces abundant seeds and pollen several years before it reaches harvest age. The taller the tree, the farther the dispersal distances. The older the tree,

the greater seed and pollen production becomes. The scale of gene flow is too great to be deterred by biocontainment zones. Placing a 1-km biocontainment zones around the perimeter of every transgenic plantation requires excessive use land and even so, the risk of transgenic escape would still be high.

Certainty of escape leads us to examine the consequences of escaped transgenic pollen and seed. Here lies another distinction for commodity conifers which tend to be weedy colonizers (HOLM 1979). In southern Africa, transgenic escapes will thrive in less managed ecosystems without human intervention as a result of deliberate genetic diversity retention and recent domestication. Domesticated conifers have no breed structure or inbred lines. They are one to three generations removed from their wild conspecifics (WILLIAMS *et al.*, 1994; MCKEAND *et al.*, 2003). In the case of indigenous conifers, one must also consider the high potential for interspecific hybridization. Compare this to U.S. food crops such as maize, cotton and soybeans which have no wild or weedy relatives in the vicinity, making gene flow from transgenic varieties less likely.

Life history is only one source of relevant distinctions between transgenic conifers and food crops. Production or silvicultural systems as well as landownership objectives also play into the decision to commercialize transgenic conifers. High-yield plantations can be adjacent to less managed or even unmanaged forest lands. Neighboring ownerships may prove problematic to those planting transgenic conifers if technology adoption rates vary widely among landowners.

Another risk determinant is the type of transgene. DNA constructs can come from genes discovered in organisms other than conifers (heterologous constructs) or from genes discovered in the same taxon (homologous constructs). DNA constructs are also classified based on perceived risk (STRAUSS 2003). The higher-risk groups include toxin genes, allergenic pharmaceutical genes or even pesticidal genes. The class with the least direct ecological impact is hypothesized to be domestication transgenes (STRAUSS 2003).

This framework shown by contrasting of two extreme examples (Table 1). Example 1 is an exotic species characterized by short rotations, sparse or delayed reproduction and perhaps facultative or obligate self-pollination. If this set of life history characters is coupled with a prevalence of high-yield private forests and long-term commitment to forest ownership then Example 1 becomes a case where transgenics are chosen as a part of the technology portfolio. Contrast this with the more recalcitrant Example 2 in Table 1. Indigenous conifers with close relatives, early reproduction, windborne seed and pollen, long rotations coupled with a prevalence of public forest ownership raise probability of ecological risk. A milder variant on Example 2 can be examined more closely using *Pinus taeda* in the southeastern United States.

Table 1. Factors affecting decision to commercialize transgenic trees shown with two opposing examples.

Factors	Example 1	Example 2
Species source	Exotic introduction	Indigenous
Sympatric relatives	None	Many
Pollination system	Selfing	Outcrossed wind-
		pollination
Seed dispersal system	Close-range animal	Windborne
	dispersal	
Onset of reproduction	Late	Early
Type of propagules	Seeds	Vegetative and seeds
Abundance of	Sparse, masting species	Abundant annual
propagules		production
Rotation age	Short	Long
Land ownership type	Private	Mixed or public
Ownership commitment	Long-term	Shorter than full rotation
Neighboring ownership	Private,	Public forest owners and
	intensivelymanaged	small woodlot owners
	plantations	
Type of transgenes	Domestication genes;	Toxin genes; Heterologous
	homologous constructs	constructs

2. PINUS TAEDA AS A CASE STUDY

Pinus taeda is selected here as a less extreme variant of Example 2 (Table 1) and it is less extreme because domestication transgenes, not toxin transgenes, are the norm. It is a wind-pollinated indigenous species characterized by abundant reproduction via seed starting after the age of 10 to 15 years, well before its rotation age of 25 to 35 years. Its range is widespread, extending throughout the southeastern United States from Maryland to Florida and to Texas. Several sympatric relatives within its Australes subsection have ranges which overlap with Pinus taeda. Its share of the world's market in timber production has now reached 15.8%; the southeastern United States produces more timber than any other country in the world (WEAR AND GREIS 2002). Forest ownership in southeastern U.S. is a mosaic of private and public landowners. Over 89% of the timberlands are privately held and small woodlot owners are the predominant owners (WEAR AND GREIS 2002). Production increases have been dramatic over the last few decades and the addition of genetic improvement to the Pinus taeda technology portfolio has added substantially to increased yields (MCKEAND et al., 2003). No transgenic plantations exist although field testing for transgenic *Pinus taeda* is extensive. The most technology-intensive portfolio for plantation forestry is still a rarity even among timber companies so

commercial use of transgenic plantations can be envisioned as a set of small foci amidst a mosaic of private and public *Pinus taeda* forests.

2.1. Technology breakthroughs enabling molecular domestication

Molecular domestication for *Pinus taeda* has become feasible due to breakthroughs in somatic embryogenesis and genetic modification. Somatic embryogenesis is a process by which a single genotype can be cloned into millions of trees. In theory, genetic modification of a single genotype which is then cloned by somatic embryogenesis makes large-scale use of transgenic pines possible in the near future. Biotechnology firms such as Arborgen and CellFor are offering clonal *Pinus taeda* seedlings to timber companies. No transgenic plantations exist yet but the approach of commercialization can be measured in the increasing numbers of transgenic field trials (MANN AND PLUMMER 2002). Molecular domestication of *Pinus taeda* plantations is technically feasible on a large scale. Testing has focused on wood quality, a source of domestication genes for transgenic *Pinus taeda*.

Molecular domestication with somatic embryogenesis and genetic transformation represents a departure from conventional domestication. Widespread use of clonal *Pinus taeda* forests with or without transgenes could narrow the numbers of genotypes, opening the question of how to protect genetic diversity of undomesticated *Pinus taeda* and its close relatives. This emerging issue deserves closer scrutiny because the federal government has contributed so little to collective genetic improvement. As a result, domesticated *Pinus taeda* germplasm is mostly privately owned by timber companies and more recently, institutional investors. A few state agencies share germplasm with these corporate owners.

Public repositories or gene conservation programs formalized by the federal government are needed as a counterbalance for molecular domestication. Gene conservation is an insurance policy against transgenic mistakes or genetic bottlenecks caused by cloning too few genotypes. In the case of *Pinus taeda*, starting a federally funded gene conservation program protects against any chances that highly domesticated or transgenic conifers prove poorly adapted outside intensively managed plantation systems.

2.2. Transgenic pollen and seed move long distances

Transgenic *Pinus taeda* is outcrossing wind-pollinated, producing an abundance of unwanted pollen and seeds. Perennial production of seeds and pollen, occurring years before timber harvest, adds up to complex gene flow dynamics. Transgenic seeds and pollen move by way of two separate processes (HENGEVELD 1989). The first process is local neighborhood dispersal (LND) which accounts for 99% of the seeds and pollen falling near source. The second process, long-distance dispersal (LDD), accounts for a tiny fraction (1%) of escaped seeds or pollen yet poses the greatest ecological concern. LDD seeds and pollen are vertically uplifted above the forest canopy by air currents then move on the order of kilometers from source.

Consider that a fraction of seeds uplifted above the forest canopy can move as far as 11.9 to 33.7 kilometers from source (NATHAN et al., 2002). Out of 10⁵ seeds

produced per hectare per year in a 16-year old plantation, roughly of those 70 seeds will reach distances in excess of 1 km from the source, a distance too great to serve as an biocontainment zone (WILLIAMS *et al.*, 2006). The value of biocontainment zones are apparent for hardwood species (LINACRE AND ADES 2004) but negated by the greater dispersal scale for conifers. Although 99% of *P. taeda* seeds and pollen fall near the source tree, it is the remaining 1.0% which poses the greatest ecological concerns. Transgenic *P. taeda* seeds and pollen moving in less managed areas, public or privately owned, can establish remote satellite colonies.

If the transgene is favored by selection, then only a small fraction of dispersed seeds will cause its spread (MEAGHER *et al.*, 2003). To be harmful, the transgenic phenotype must exhibit increased invasiveness properties compared to its wild-type. Genes conferring increased invasiveness can result in displacement of local endemic species or even maladaptation (LEE 2003). Ecological risks are critical if invasiveness is increased in transgenic conifers.

2.3. Hybridization between transgenic Pinus taeda and its close relatives

So far, discussion has centered on gene flow between domesticated and undomesticated *Pinus taeda*. Natural hybridization does occur between *P. taeda* and its numerous relatives in the southeastern US although phenological conditions rarely overlap among species from year to year. For example, close relative *Pinus serotina* hybridizes with *Pinus taeda* on rare occasion (SAYLOR AND KANG 1973). Hybrids can freely cross with the two parental species or even a third species so the transgene may remain segregating in the gene pool indefinitely. Unless transgenic *P. taeda* trees have altered phenology, genetic swamping of related species by transgenic *P. taeda* has low probability but potentially high impact if the transgene confers higher fitness to the hybrid seedlings.

2.4. Exploring regulatory reform

Federal regulation of transgenic *Pinus taeda* as field tests or commercial plantations will continue given the unknown nature of ecological risks. Regulation of transgenic organisms has matured since inception of a tripartite government regulatory entity among three agencies: USDA, EPA and FDA. Primary responsibility resides with USDA-APHIS's Biotechnology Regulatory Services who recognizes that one set of regulations no longer fits all transgenic plants so U.S. regulatory reform is underway for transgenic conifers.

To aid this effort, several focus groups during our 2004 Nicholas School Leadership Forum *Landscapes, Genomics and Transgenic Conifers* were asked to evaluate four hypothetical regulatory options and results shown here were first summarized in our conference report. Continued regulatory oversight was a common response (Table 2). One individual voiced a need for a fourth option, a permanent moratorium for transgenic forest trees.

Table 2. Pros and cons of four hypothetical options for regulating transgenic or genetically modified (GM) forest trees.

Option	1) Moratorium	2) Research Agenda	3) Relaxed Regulations	5) Free Market
Description	Halt outdoor planting of GM confers for ten years on public and private lands. Permit laboratory and greenhouse research.	Continue to test GM conifers with domesticated neogenes in field tests under current APHIS regulations. Shift priority for competitive funding to exploratory research on other genomic applications suited to a wide range of silvicultural applications.	Allow certain GM field trials to reach timber harvest age in order to assess full benefits. These selected trials will test trees with DNA constructs only from functional genes discovered in conifers.	Remove government regulation. GM seedlings can be sold for-profit to any customer who wants to buy them.
Pros	No risk of seed or pollen escape	Stimulates new funding for forest tree genomics	Benefits from current investment in R&D pipeline realized	Benefits from current investment in R&D pipeline realized
	Technology develops during moratorium. For example, can test for unintended effects	Allows time to shift investment into new areas without losing materials in current pipeline	Timber and seedling industry can stay competitive in global markets	Timber and seedling industry stay competitive in global markets
	Provide time for public input	Acquire real data for benefits analysis	Acquire better data on gene flow data from GM trees for a full rotation	Industry forced to self-regulate
	Potential harm suspended	Increased funding for marker- assisted breeding and for functional genomics	Test methods for reproductive sterility	Reduced cost of final product, decrease time to market
	More time to identify societal benefits	Increased research funding		
	Basic research focus will be deepened with less pressure on immediate application			

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Cons	Consider release and field testing in Southern Hemisphere where there are no indigenous pine forests All transgenes do not have the same adverse (or beneficial) effects	Stifles GM research	Potential benefits suspended yet potential harms not avoided	Early adopters could face unforeseen problems without data collection, tracking or regulatory oversight
	Cost borne by private sector	Current regulations are inadequate for preventing escape of GM pollen and seeds	Increased gene flow from GM conifers	Effect on indigenous forests questionable due to high rate of transgenic escapes from commercial plantations
	Current investment in R&D pipeline wasted	Current regulations would have to be changed to allow reproduction	International embargo against GM timber from US	GM timber might meet with embargo on world market
	No field data would be available at the end of the moratorium for calibrating regulations	Too little competitive funding even at this time so not likely to have enough to research or develop genomics alternatives		Setting bad precedent for any other technology or methods for producing novel organisms
	Potential benefits suspended	No emphasis on forest genomics funding as is. Research funding occurs in the for- profit sector.		Buyer obligations and liability are unclear so harm will not borne by those who benefit financially
	Subversion of investor commitment	Decrease private investment		Untested risks from gene flow
	Other countries have less regulatory restriction and will capture market	Delay benefits from forest biotechnology by starting other avenues of inquiry		Increase in legal action and litigation
	Decreased funding for research			Patchwork of local and state regulations would restrict GM trees and this is the wrong scale for

		biotechnology governance
Create backlog in R&D pipeline which would release an huge amount of regulatory works after moratorium is over		governance
Permanent ban is needed for GM forest trees because they exceed our limits of biotechnology governance; no regulatory oversight would be a cost savings		

2.5. Exploring future scenarios for commercial use of transgenic Pinus taeda

Regulatory reform carries several implicit assumptions about use of transgenic conifer technology. Exploring future scenarios offers some insight about the validity of regulation. Two likely scenarios fit: 1) transgenic technology is not commercialized for *Pinus taeda* and 2) transgenic technology deregulation. Evaluating these served as a means of introducing a third intermediate scenario: starting a technology trust to ensure sound use of transgenic *Pinus taeda*.

The first scenario predicts commercial use of transgenic technology could be reduced or even abandoned for *Pinus taeda* if the trend towards timber company land divestiture continues. Recent sales of U.S. timberlands to institutional investors points to less intensively managed forest plantations. In 2005 alone, Boise Cascade sold 891,000 hectares of U.S. timberland to Forest Capital Partners LLC; the sale includes a long-term wood supply agreement for Boise's mills. Likewise, MeadWestvaco Corp. divested 360, 000 hectares of its timberlands to a private investment firm, Cerberus Capital Management. Less intensively managed timberlands might be expected in the future because the high costs of genetically enhanced seedlings or emblings incurred at plantation establishment must be carried through rotation. If the new institutional buyer wants to maximize profit from supplying wood to the seller, then less costly regeneration practices seem likely. If the standing timber is sold by the new buyer before harvest then genetic enhancements will also represent a loss because the timberland value is the same with or without genetic enhancements.

To illustrate this point, genetically enhanced emblings cost more than the fivecent *Pinus taeda* seedling sold today. Biotechnology firms are offering clonal seedlings or somatic emblings to timber companies and the price of a somatic embling is thought to be at least eight to ten times higher than a seedling. Price of a genetically modification to somatic emblings will be even higher in order to obtain a return on research, development and regulatory costs unless costs are offset by increased production efficiency or volume sales. Volume sales for *P. taeda* planting stock are low at 1 billion trees annually and seem unlikely to expand with offshore planting. Success of *Pinus taeda* as an exotic has been limited (BRIDGWATER *et al.*, 1997) and even curtailed by successful introduction of several Mexican and Central American pine species (DVORAK *et al.*, 1996). One might conclude that adding transgenic trees to the technology portfolio for *Pinus taeda* will be curbed by trends towards U.S. timberlands divestiture. Will timberland divestiture diminish chances of transgenic technology adoption for *Pinus taeda* in the southeastern United States?

The second likely scenario predicts deregulation. One can argue stringent U.S. regulations could provide incentive for multinational timber companies to plant transgenic forest plantations in South America rather than in North America. Given a profitable outcome for these Southern Hemisphere transgenic plantings, political pressure will mount to introduce transgenic conifer technology in North America and with this pressure will come demands for transgenic deregulation. Otherwise, cost of regulation will be too high to extract profits from local seedling markets and global wood products consumers alike. Will pressure to deregulate come from other countries with no regulations or relaxed forest certification flooding the world's markets with cheaper wood?

A second argument for deregulation is based on low public awareness in the United States. The issue of transgenic *Pinus taeda* falls outside of the issue-attention cycle for the following reasons: 1) too few citizens suffer enough on daily basis to stay riveted to the problem, 2) profits are at stake for a powerful minority of multinational corporations, 3) the timescale for adverse impact of transgene escape is beyond comprehension and 4) the problem lacks dramatic qualities to make it newsworthy. Low public awareness coupled with increasing scientific illiteracy adds up to no political interest in the outcome. Without political interest, research on ecological risks will not receive priority in competitive federal programs and without ecological risks data, one is left with intuitive arguments dismissing potential harm rather than the objective outcome from experimental data. In short, low public awareness seems a likely outcome because forests are rural, remote and scenic to urban dwellers. Who among us will know or even care if transgenic forests are even planted?

A third argument for deregulation can be made on the basis of pragmatism: that regulation of transgenic conifers in the absence of reproductive sterility will prove costly but futile. Tracking transgenic plantations bought and sold before harvest age will be prone to regulatory failure. Compliance can fail due to attrition, poor records, mergers and acquisitions so that lost transgenic plantings are abandoned. If their location is proprietary then location may not be disclosed as part of the sale. Even if a transgenic plantation is tracked, regulation will be costly but only be nominal due the sheer volume of escaped seeds and pollen. Is transgenic *Pinus taeda* a resource which cannot be truly contained, tracked or regulated?

3. A TECHNOLOGY TRUST OPTION FOR PINUS TAEDA

A public-private partnership or a technology trust is proposed as an alternative to the deregulation scenario. Focus group results shown in Table 2 suggests a public-private partnership might be favored as a vehicle for evaluating transgenic *Pinus taeda* for commercial use. A technology trust has three components: 1) a federal gene conservation program as a hedge against molecular domestication, 2) a technology tax on transgenic field testing which carries a hold-harmless provision to the payee or protection against future liability claims and 3) a designated subset of transgenic field tests would become long-term study sites for collecting relevant data for sound benefits and risk analyses. Relevant data on benefits and risk analysis would be made publicly available, thus providing an outlet for public dialogue. Such a technology trust could be designed and run with scientific oversight from government, university and private-sector research organizations.

A possible drawback to a technology trust is that its public-private scientific partnership could slow or even halt private investment in North America and Europe. Timber companies may not welcome public participation in its research agenda. Its commitment to research tends to rise and fall so sustaining a technology trust could a problem in this market sector. Without corporate interest, a technology trust will fail. Although it offers public relations value in the short-term, its true scientific contribution depends on sustained corporate commitment to landownership within a given geographic region and to high-yield forestry practices.

Direct benefits are that studies conducted under the technology trust would be re-evaluated at specific intervals and they would require a formal outlet for public dialogue. The public forum would bring a sharper focus to relevant goals, strategic experimental designs and efficient data collection. The added transparency to technology portfolio decision-making would provide a needed conduit for public deliberation within a time-sensitive framework. Public deliberation would raise needs for specialized knowledge for landowners, business managers, foresters and environmental activists. Genetic composition is a matter of good stewardship yet this topic has received less attention in classroom and in continuing-education venues than it deserves. It deserves more professional education than merely updating curricula for students enrolled in college and university classrooms.

In summary, a technology trust for *Pinus taeda* in the southeastern United States is proposed as a model program for providing sound benefits-risk analysis, initiating a gene conservation program, addressing long-term liability claims and sharpening relevant public dialogue. The price for adding transgenics to its technology portfolio for increasing plantation productivity without this timely information has yet to be determined.

4. CONCLUSIONS

Private investment can fund the creation of novel transgenic trees at a rate that will outpace scientific assessment of environmental concerns. Public-sector funding of ecological research has not kept up for several reasons, perhaps because transgenic

conifers incorrectly viewed as a type of transgenic food crop. Transgenic conifers do in fact differ in a number of important ways, including 1) a wider radius for pollen and seed movement, 2) recurring and abundant seed and pollen production from each plant which begins years before its harvest and 3) diverse objectives and production systems in adjacent forest ownerships.

Major factors driving the decision to use transgenic conifers on a commercial scale are 1) reproductive systems of the forest species and 2) landownership profiles and 3) types of transgenes. To illustrate this point, a case study for *Pinus taeda* is presented. Two future scenarios of technology abandonment and technology deregulation were explored then followed by proposal of a technology trust, which was defined as a public-private partnership for evaluating transgenic *Pinus taeda* commercialization. The Technology Trust would provide a formal gene conservation program, address liability claims, serve as a formal outlet for benefits-risk analysis and open an outlet for better public dialogue. Public dialogue in turn would prompt better education about genetic composition for landowners, environmental activists and foresters alike. Under certain conditions, a technology trust could lead to maintaining healthy, well-adapted indigenous forests.

5. REFERENCES

BESSEY, C. 1883. Remarkable fall of pine pollen. American Naturalist 17:658.

BRIDGWATER, F.E., R.D. BARNES AND T. WHITE. 1997. Loblolly and slash pines as exotics. pp. 18-32. In Proceedings of the 24th Southern Forest Tree Improvement Conference, Orlando Florida June 9-12, 1997.

FRIEDMAN S.T. AND G.S. FOSTER. 1997. Forest genetics on federal lands in the United States: public concerns and policy responses. *Canadian Journal of Forest Research* 27(3): 401-408.

DVORAK W.S. AND J.K. DONAHUE. 1992. CAMCORE Cooperative Research Review 1980-1992. North Carolina State University, Raleigh North Carolina.

HENGEVELD, R. 1989. Dynamics of biological invasions. Chapman and Hall, London. 160 p.

HOLM L., J.V. PANCHO, J.P. HERBERGER AND D.L. PLUCKNETT. 1979. A geographical atlas of world weeds. John Wiley and Sons, New York. 391 p.

LEE, C.E. 2002. Evolutionary genetics of invasive species. *Trends in Ecology and Evolution* 17: 386-391. LINACRE N.A. AND P.K. ADES. 2004. Estimating isolation distances for genetically modified trees in plantation forestry. *Ecological Modelling* 179: 247-257.

MANN, C.C. AND M.L. PLUMMER. 2002. Biotechnology – forest biotechnology edges out of the lab. Science 295: 1626-1629.

McKeand S.E., T. Mullin, T. Byram and T. White. 2003. Deployment of genetically improved loblolly and slash pines in the South. *Journal of Forestry* 101 (4/7): 32-37.

MEAGHER, T.R., F.C. BELANGER AND P.R. DAY 2003. Using empirical data to model transgene dispersal. *Philos. Trans. R. Soc. Lond. B* **358**: 1157-1162.

NATHAN, R, G.G. KATUL, H.S. HORN, S.M. THOMAS, R. OREN, R. AVISSAR, S.W. PACALA AND S.A. LEVIN. 2002. Mechanisms of long-distance dispersal of seeds by wind. *Nature* 418: 409-413.

SAYLOR L.C. AND K.W. KANG. 1973. A study of sympatric populations of *Pinus taeda* L. and *Pinus serotina* Michx. in North Carolina. *Journal of Elisha Mitchell Society* 89: 101-110.

SEDEROFF, R., A. STOMP, B. GWYNN, E. FORD, C. LOOPSTRA, P. HODGKISS AND W.S. CHILTON. 1987. Application of recombinant DNA techniques to pines: a molecular approach to genetic engineering in forestry. Chapter 19. In Cell and Tissue Culture in Forestry, vol. I (J.M. Bonga and D.J. Durzan, eds). Nijhoff Publishing. Leiden, The Netherlands.

STRAUSS, S.H. 2003. Genomics, genetic engineering and domestication of crops. Science 300: 61-62.

WEAR D.N. AND J.G. GREIS. 2002. Southern Forest Resource Assessment: summary of findings. *Journal of Forestry* 100: 6-14.

WILLIAMS, C.G., J.L. HAMRICK AND P.O. LEWIS. 1994. Genetic diversity levels in a multiple population breeding strategy: a case study using *Pinus taeda* L. *Theoretical and Applied Genetics* **90**:384-394. WILLIAMS, C.G. 2005. Framing the issues on transgenic pine forests. *Nature Biotechnology* **23**: 1-3. WILLIAMS, C.G., S.L. LADEAU, R. OREN AND G.G. KATUL. 2006. Modeling seed dispersal distances: implications for transgenic *Pinus taeda*. *Ecological Applications* (in press).